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Genetic diversity of midwestern oat germplasm

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TABLE OF CONTENTS

INTRODUCTION

The presence of genetic diversity within a species is crucial to sustained progress from selection for productivity, resistance of the species to diseases and pests, and stability of production over time. Quantifying the diversity present within a species is of interest to breeders for two reasons: 1) so that it may be maintained or increased over time and 2) to aid in the selection of parents for breeding programs. Numerous procedures for quantification of genetic variability are available which use molecular, genic, genotypic, or phenotypic measurements.

Rodgers et al. (1983) examined the relationship between genetic diversity as measured by coefficient of kinship (Malecot, 1969) and grain yield improvement in spring oats (Avena sativa L.). They indicated that recently developed, high-yielding cultivars represented several distinct sources of germplasm. These cultivars originated from four breeding programs in the midwestern USA.

My study was undertaken to quantify the genetic diversity among genotypes from these four programs. The objective was to evaluate, in an empirical manner, the relationships of four measures of genetic distance with heterosis, transgressive segregation, and generalized genetic variances.

LITERATURE REVIEW

Molecular Measures of Genetic Diversity

The most appropriate measure of genetic diversity is the number of nucleotide or codon differences per unit length of DNA (Nei, 1974). Goodman and Laaker (1974) defined genetic distance between two populations as: the proportion of nonmatching nucleotide bases at homologous nucleotide sites in the two genomes. They state further that since the matching nucleotide bases in these genomes are identical by descent from a common ancestor, genetic distance also measures genetic or phylogenetic divergence. Using amino acid sequences from corresponding proteins in the two populations, similar procedures may be applied to calculate genetic distance (Fitch and Margoliash, 1967; Doolittle and Blomback, 1964).

Allelic frequencies at marker loci also can be used to measure genetic diversity. With this procedure, each population is characterized by a vector of frequencies of alleles at a single locus. To summarize marker-gene data, Cavelli-Sforza and Edwards (1967) proposed two distance measures. The first measure of distance for populations i and j is

$$arc(ij) = 2/\pi \arccos\textstyle\sum_r (p_{ir}p_{jr})^{1/2}, \text{ and}$$

the second is

$$chord(ij) = [2(2)^{1/2}/\pi](1-\textstyle\sum_r (p_{ir}p_{jr})^{1/2})^{1/2},$$

where p_{ir} and p_{jr} are the frequencies of the r^{th} allele in populations i and j, respectively. Jacquard (1974) proposed the use of a chi-square distance measure where

$$X^2(ij) = \Sigma_r(p_{ir}-p_{jr})^2/\bar{p}_r,$$

in which

$$\bar{p}_r = \Sigma_i n_i p_{ir}/\Sigma_i n_i,$$

and p_{ir} and p_{jr} are defined as above. The chord metric of Cavalli-Sforza and Edwards (1964) and the chi-square metric of Jacquard (1974) can each be extended to any number of loci. For s loci ($s \geq 2$),

$$G^2(ij) = \Sigma_s[\text{chord}_s(ij)]^2$$

and

$$X^2(ij) = \Sigma_s X_s^2(ij).$$

An alternative distance measure was proposed by Nei (1974) and was, essentially, minus the natural log of the normalized identity of genes between two populations.

Distance Based on Known Ancestry

Several genetic probabilities can be estimated, either directly or indirectly, if the ancestries of individuals are known. An example is Malecot's coefficient of kinship, which is defined with respect to two individuals, A and B, as the probability that a random allele from A is identical by descent with a random allele from the homologous locus in B (Malecot, 1969). Given a pedigree and assuming no selection and non-inbred, unrelated ancestors, coefficients of kinship can be calculated between all pairs of individuals (Kempthorne, 1969). Jacquard (1974) defined the genetic distance between individuals A and B as $D(AB)=1-\Phi_{AB}$,

where Φ_{AB} is the coefficient of kinship. In addition to the coefficient of kinship, nine other probabilities of identity by descent can be calculated for a pair of individuals. These were called "condensed coefficients of identity" by Cockerham (1971) and Jacquard (1966); however, they were first defined by Harris (1964) and Gillois (1964). Using condensed coefficients of identity, Jacquard (1974) defined genealogical distance between A and B as:

$$G(AB) = 1-(\Phi_{AB}+1/2\Delta_7+1/12\Delta_8),$$

where Φ_{AB} is the coefficient of kinship of A and B, and Δ_7 and Δ_8 are two of the condensed coefficients of identity. Jacquard (1974) stated that any monotonic function of either D(AB) or G(AB) could also be employed as a distance measure.

Coefficients of kinship have been used to quantify the genetic diversity among released cultivars of a species. This method was used by St. Martin (1981) and Delanney et al. (1983) for soybeans (Glycine max L.) and by Rodgers et al. (1983) and Baum and Lefkovitch (1973) for oats.

A criticism of using coefficient of kinship to measure genetic diversity is that the original parents may be related. MacCluer et al. (1983) indicated that the effect of remote inbreeding on coefficient of kinship depends upon the effect that the trait of interest has on fitness. Alleles that contribute to reproductive fitness are more likely to be identical by descent than are neutral alleles, and remote inbreeding is more apt to cause identity by descent for such favorable alleles.

Phenotypic Measures of Diversity

A third approach to quantifying the genetic diversity among populations utilizes phenotypic data. The effectiveness of this approach depends upon how closely phenotypic and genotypic measurements are correlated.

Basic distance measures include Pearson's Coefficient of Racial Likeness (CRL) (Pearson, 1926; Goodman, 1972) and Sokal's distance (Sokal, 1961; Goodman, 1972). The CRL was developed for traits for which the measurements are normally distributed, while Sokal's distance was developed to handle character scores. Both ignore correlation between traits and require standardization of measurements. Sokal's distance between two populations A and B is

$$D(AB) = [1/p\sum_{i}^{}(x_{iA}-x_{iB})^2]^{1/2}$$

where x_{iA} and x_{iB} are the standardized scores of A and B for character i, respectively, and p is the number of characters. The formula for the CRL is

$$CRL(AB) = 1/p\sum_{i}^{}(x'_{iA}-x'_{iB})^2-1/p$$

where x'_{iA} and x'_{iB} are the standardized values for trait i of A and B, respectively, and p is the number of traits; this formula requires equal sample sizes. A distance measure that takes correlations among traits into account was developed by Mahalanobis (1936). The formula for Mahalanobis' generalized distance between two populations A,B, as given by Rao (1952), is

$$D(AB) = [(\underset{\sim}{X}_A - \underset{\sim}{X}_B)' R^{-1} (\underset{\sim}{X}_A - \underset{\sim}{X}_B)]^{1/2},$$

where $\underset{\sim}{X}_A$ and $\underset{\sim}{X}_B$ are p dimensional vectors of means for A and B, respectively, and R^{-1} is the inverse of the correlation matrix for the p traits. Several other measures of diversity based on phenotypic data have also been defined (Goodman, 1972).

Rotation of the axes of the original data to obtain a set of orthogonal, uncorrelated axes is accomplished by using principal component analyses. Euclidean distance may be calculated using scores on the principal component axes. The distance between two populations A and B is given by:

$$D(AB) = [\sum_{i=1}^{k} (y_{iA} - y_{iB})^2]^{1/2}, \quad k \leq p,$$

where y_{iA} and y_{iB} are the values for the i^{th} principal component for A and B, respectively (Gower, 1966). Using all principal components (i.e. k=p) in this formula gives distances identical to those measured using the original traits. However, in most applications, only two or three principal components are included (Goodman, 1972; Adams, 1977; Cox, 1983).

Measures of Diversity Based on Breeding Behavior

Hanson and Casas (1968) developed two measures of genetic diversity based on an n-parent diallel. Both located the parents on an orthogonal set of axes, followed by calculation of Euclidean distance. The first measure achieved orthogonalization of axes by using a set of n-1 orthogonal contrasts. The position of each parent on each axis was standardized, followed by calculation of Euclidean distance. Hanson and Casas

(1968) demonstrated that the distance obtained is independent both of the order of parents in the diallel or the set of orthogonal contrasts used.

The second measure proposed by Hanson and Casas (1968) involved obtaining a symmetric matrix of specific combining ability effects, S. Principal component analysis was computed for S, and euclidean distance was then calculated on the principal component values.

Cervantes et al. (1978) proposed three measures of genetic diversity that utilized data from diallels, one that used general combining ability (GCA) effects, one that used specific combining ability (SCA) effects, and one that used both GCA x environment and SCA x environment effects. The three genetic distance measures proposed by Cervantes et al. (1978) were obtained by taking the correlations among parental populations, based on standardized genetic and genotype by environment interaction effects. The distance between two parents A,B in each instance was obtained as

$$D(AB) = 1-r_{AB},$$

where r_{AB} is the correlation between A and B.

Breeding Behavior of Interest

A breeder may be interested in any or all of the following types of breeding behavior that relate to a set of parents: (a) mean performance of the parents per se, (b) mean performance of F_1 hybrids between the parents, (c) mean performance of inbred generations of matings among parents, (d) genetic variability within the parents per se, (e) genetic variability in inbred generations of matings, (f) relationships among traits within the parents and within the inbred generations of matings

(Moll and Stuber, 1974; Falconer, 1981; Hallauer and Miranda, 1981). Types (b) and (c) have shown the closest association with known diversity of the parents (Moll and Stuber, 1974; Goodman, 1968).

Heterosis was positively associated with genetic diversity of the parents in cotton (Gossypium spp.) (Marani, 1963; Marani and Avieli, 1973), alfalfa (Medicago spp.) (Sriwatanapongse and Wilsie, 1968), oats (Avena spp.) (Jenkins, 1968), winter wheat (Triticum aestivum L. em Thell) (Fonesca and Patterson, 1968), spring wheat (T. aestivum L. em Thell) (Sun et al., 1972), durum wheat (T. turgidum L. var. durum) (Widner and Leabock, 1973), and maize (Zea mays L.) (Moll et al., 1962; Paterniani and Lonnquist, 1963). However, studies in maize and tobacco (Nicotiana tabacum L.) (Moll et al., 1965; Matzinger and Wernsman, 1967) have shown that the relationship between heterosis and genetic diversity is not always linear, with some matings between very distantly related parents exhibiting little or no heterosis.

Variability expressed among inbred segregates from matings is a direct genetic test of the diversity of the parents (Goodman, 1969). The relationship between genetic variation within matings and genetic divergence of parents should be nondecreasing. Hence, all other measures of genetic diversity, if they reflect real diversity, will be positively associated with the genetic variability within matings.

A second type of breeding behavior associated with genetic diversity among parents is the occurrence of transgressive segregates (Smith, 1966; Baracki et al., 1976; Frey, 1976; Lawerence and Frey, 1976). Transgressive segregates as defined by Darlington and Mather (1949) are

those genotypes in a segregating generation that fall outside the limits of parental and F_1 values. In most recent uses of the term, the parental range only is used.

Few studies have been designed to address the relationship between genetic diversity of the parents and transgressive segregation of progeny. Cox (1979) evaluated transgressive segregation for protein percentage in inter- and intraspecific matings of oats and found higher numbers of transgressive segregates occurred in matings of more distantly related parents. Cox and Frey (1984) obtained similar results for the traits biomass, grain yield, and vegetative growth index. Vega and Frey (1980) evaluated transgressive segregation in inter- and intraspecific matings in barley (Hordeum spp.) and observed higher frequencies of transgressive segregates for grain yield in matings of more distantly related parents. However, higher frequencies of transgressive segregates for heading date, plant height, bundle weight, and harvest index occurred in matings of less distantly related parents.

Relationship Between Measures of Diversity and Breeding Behavior

In most studies that have related breeding behavior to genetic diversity, the assumed diversity was based on examination of pedigrees, knowledge of ancestral relationships, geographic origin, obvious morphological differences, or species designation of the parents used. Where quantified measures have been used, only the distance measure-heterosis correlation or regression was examined.

Hanson and Casas (1968) observed a close positive association between heterosis for grain yield and the genetic distance measure, R(AB), in

maize, but the relationship was not strictly linear. Isilieb and Wynne (1983) evaluated 27 matings of exotic peanut (Arachys hypogea L.) introductions crossed to an adapted cultivar and evaluated the regression of heterosis on Euclidean distance based on principal components between the parents. For five traits, positive linear regression coefficients were observed with R^2 values ranging from 0.14 to 0.44, whereas for three traits, negative linear regression coefficients were observed with R^2 values ranging from 0.17 to 0.61. The trait with negative regressions had positive quadratic coefficients.

Ghaderi et al. (1984), working with dry bean (Phaseolus vulgaris L.) and faba bean (Vicia faba L.), computed correlations between Mahalanobis' D^2 and heterosis for a number of traits. With dry bean, they evaluated an eight-parent diallel and found that for five traits the correlations were positive and significant (0.54 to 0.73) and for three trait correlations were negative and nonsignificant. With faba bean, they also evaluated an eight-parent diallel and showed positive and significant correlations for six traits (0.43 to 0.82) and negative and significant correlations for five (-0.31 to -0.76).

PART I. THE RELATIONSHIP BETWEEN GENEALOGICAL DISTANCE AND HETEROSIS, TRANSGRESSIVE SEGREGATION, AND GENERALIZED GENETIC VARIANCES IN OATS

ABSTRACT

Eight oat cultivars and experimental lines from four germplasm sources were crossed in a diallel mating design without reciprocals. F_1 heterosis for grain yield was evaluated in two experiments, and 48 F_2-derived lines from each of the 28 matings were evaluated for bundle weight, grain yield, straw yield, harvest index, height, and heading date in two experiments. Number of transgressive segregates per trait and generalized genetic variance were calculated for each mating. Genealogical distance for each mating was obtained using coefficient of kinship based on the pedigree of the parents. The relationship between genealogical distance and the three types of breeding behavior was examined via correlation and regression. Significant correlations occurred only for genealogical distance with numbers of transgressive segregates for height and with generalized genetic variances. Both were positive. Significant heterosis was observed for matings of more distantly related parents. Regressions on genealogical distance, where significant, were linear. Genealogical distance between parents was positively associated with diversity based on breeding behavior.

INTRODUCTION

Recently, several researchers have used coefficients of kinship (Malecot, 1969) to quantify the genetic diversity among a set of cultivars of a given species. Coefficients of kinship were based upon published pedigrees, assuming that the original parents in the pedigree were unrelated. This procedure was used by St. Martin (1981) and Delanney et al. (1983) for soybeans (Glycine max (L.) Merr.) and Rodgers et al. (1983) and Baum and Lefkovitch (1973) for oats (Avena sativa L.).

Jacquard (1974) proposed two measures of genetic distances based on probabilities. The first measure of distance between two parents, A and B, was D(AB)=1- AB, where AB is the coefficient of kinship of A and B. The second distance measure, called genealogical distance, was G(AB)= $1-(\Phi AB+1/2\Delta_7+1/12\Delta_8)$, where Φ_{AB} is the coefficient of kinship and Δ_7 and Δ_8 are two of the condensed coefficients of identity. If A and B are fully inbred, then $\Delta_7=\Delta_8=0$ and D(AB)=G(AB). Any monotonic function of D(AB) or G(AB) can serve as a measure of genetic distance.

Three types of breeding behavior are related to the genetic divergence of parental populations. Heterosis has been shown to be positively associated with genetic divergence of the parents in cotton (Gossypium spp.) (Marani, 1963; Marani and Avieli, 1973), alfalfa (Medicago spp.) (Sriwatanapongse and Wilsie, 1968), oats (Avena spp.) (Jenkins, 1968), winter wheat (Triticum aestivum L. em Thell) (Fonesca and Patterson, 1968), spring wheat (T. aestivum L. em Thell) (Sun et al., 1972), durum wheat (T. turgidum L. var. durum) (Widner and Lesbock, 1973), and maize (Zea mays L.) (Moll et al., 1962; Paterniani and Lonnquist,

1963). Greater numbers of progeny whose performance exceeds the parental range (transgressive segregates) have been observed in matings of more distantly related parents in oats (Avena spp.) (Cox, 1979; Cox and Frey, 1984) and barley (Hordeum spp.) (Vega and Frey, 1980). Goodman (1969) indicated that a direct genetic test of the degree of divergence of two compatible parents is the relative variability of their F_2. Goodman (1968) and Sokal (1965) have indicated that the generalized variance, or determinant of the variance-covariance matrix, was the most sensitive measure of overall variability in any segregating generation.

Rodgers et al. (1983), who examined the relationship between coefficient of kinship among parents (Malecot, 1969) and grain yield improvement in spring oats (Avena sativa L.), found that recently developed, high-yielding cultivars displayed a broad range of variability for agronomic traits and represented several distinct sources of germplasm. These cultivars originated from four breeding programs in the midwestern USA.

In this study, I investigated the relationship between genealogical distance among genotypes from the four midwestern USA oat-breeding programs and heterosis, transgressive segregation, and generalized genetic variances in matings among the genotypes. The primary objective was to determine if genealogical distance provided an adequate measure of the real diversity among genotypes from these four germplasm sources.

MATERIALS AND METHODS

Eight cultivars and experimental lines of oats that originated from breeding programs in Iowa, Illinois, Indiana, and Missouri were used to initiate this study (Table 1). All eight lines produced grain yields equal to 130% of the cultivar Gopher according to Rodgers et al. (1983) and Rodgers (D. M. Rodgers, Dept. of Agronomy, Kansas State University, personal communication, 1981).

The eight parents were crossed in a diallel without reciprocals to produce 28 matings. In 1982, 120 F_2 seeds from each mating were space planted in the field. When mature, individual F_2 plants were harvested and threshed, and the seed from a plant was used to establish an F_2-derived line. A random set of 48 F_2-derived lines was obtained from each mating for evaluation.

In addition, sufficient F_1 seed was produced of L1xL4, L1xL5, L1xL6, L1xL7, L2xL4, L3xL6, and L6xL8 to conduct replicated evaluation trials. These represent matings among parents from different breeding programs.

Field Evaluation

Four seperate experiments were conducted to evaluate the breeding behavior of the 28 matings; these are referred to as experiments I, II, III, and IV.

Experiment I

In 1983, three generations, the P_1, P_2, and F_1, of each of seven interprogram matings were evaluated in a randomized complete block design with two replicates at each of three locations: (1) the Agronomy and

Table 1. Name or accession number, breeding programs of origin, and designation of oat lines used as parents

Parent	Origin	Designation
Porter	Indiana	L1
D226-30-8	Iowa	L2
PI No. 469112	Iowa	L3
Ogle	Illinois	L4
CI No. 9273	Iowa	L5
Bates	Missouri	L6
CI No. 9277	Iowa	L7
Lang	Illinois	L8

Agricultural Engineering Field Research Center near Ames, Iowa (Agronomy Farm), (2) the Hinds Research Farm, near Ames, Iowa (Hinds Farm), and (3) the Northern Research Center near Kanawha, Iowa (Kanawha). A plot consisted of a hill sown with 20 seeds, and plots were spaced 30.5 cm in perpendicular directions. Each replication was bordered with two rows of hill plots to provide competition for peripheral plots. Fertilizer was applied preplant at per ha rates of 51.5 kg N and 7 kg each of P and K at Kanawha; 33.6 kg N and 51.5 kg each of P and K at the Agronomy Farm; and 84 kg N, 67.2 kg P and 100.8 kg K at the Hinds Farm. All plots were hand weeded. To prevent foliar diseases, an eradicant fungicide, Bayleton (1-(4-chlorophenoxy)-3,3-dimethyl-1-(1H-1,2,4-triazol-1-yl)-2-butone) was applied approximately one month prior to harvest.

Only grain yield (GYLD) was evaluated in experiment I (Table 2).

Table 2. Traits measured on a plot basis in experiments I, II, III, and IV

Trait	Designation	Definition
Heading date	HD	Number of days between June 30 and when 50% of the panicles were completely emerged
Bundle weight	BWT	Dry weight (kg/ha) of total above ground biomass
Grain yield	GYLD	Dry weight (kg/ha) of threshed grain
Straw yield	SYLD	Dry weight (kg/ha) of vegetative tissue
Harvest index	HI	Grain yield expressed as a percentage (%) of bundle weight
Height	HT	Height (cm) from ground surface to the tip of the average panicle

Experiment II

In 1984, the eight parental lines and F_1s of 27 of 28 possible matings of the diallel were evaluated in a completely randomized experiment of spaced plants at the Agronomy Farm. The F_1 of mating L3xL6 was not included. The 35 entries were randomly assigned to plots, each parental line was planted in four plots, and an F_1 in one to three plots. A plot consisted of a row 6 m long in which plants were spaced 30 cm apart and plots were spaced 1 m apart. Numbers of plants measured for the parents ranged from 54 to 73 with an average of 62, and numbers of plants measured for F_1s ranged from 3 to 51 with an average of 25. Fertilizer rates per ha were 33.6 kg N and 51.5 kg each of P and K, respectively. Only grain yield (GYLD) was measured in experiment II (Table 2). Because

spaced plant values were difficult to convert to kg/ha, the data were expressed as gm/plant.

Experiment III

In 1983, 48 F_2-derived lines in F_3 from each of the 28 matings and the parents each entered seven times were evaluated in a split plot design with two replicates at each of three locations: (1) the Agronomy Farm, (2) the Hinds Farm, and (3) Kanawha. Matings were assigned to main plots and F_2-derived and parental lines were assigned to subplots. The 48 F_2-derived lines and two parents of a mating were randomly assigned to the 50 subplots in a main plot. A plot consisted of a hill sown with 30 seeds, and plots were spaced 30.5 cm apart in perpendicular directions. A replication consisted of 1400 plots. Each replication was bordered by two rows of hill plots to provide competition for peripheral plots. Fertilizer rates per ha and disease control measures were the same as for experiment I.

The traits bundle weight (BWT), grain yield (GYLD), straw yield (SYLD), and harvest index (HI) were measured on a plot basis on all replications at all locations, height (HT) was measured on one replication at all locations, and heading date (HD) was measured on one replication at the Agronomy and Hinds Farms (Table 2).

Experiment IV

In 1984, experiment III was repeated using F_2-derived lines in F_4, with two replications at each of two locations: (1) the Agronomy Farm and

(2) Kanawha. Fertilizer rates per ha and disease control measures were identical to experiments I and III.

The traits bundle weight (BWT), grain yield (GYLD), straw yield (SYLD), and harvest index (HI) were measured on a plot basis on all replications at both locations, while height (HT) and heading date (HD) were measured on one and both replications, respectively, at the Agronomy Farm (Table 2).

Calculation of Genealogical Distances

Coefficient of kinship (Malecot, 1969) among the eight parental lines was calculated from their pedigree assuming that the earliest genotypes in the pedigree were unrelated; generally, the earliest genotypes were original introductions into the USA. Cultivars that originated as selections from the same introduction were assumed to be heterogeneous and were assigned half-sib relationships (ϕ=0.25) (Rodgers et al., 1983).

Coefficients of kinship were computed using an iterative approach similar to that described by Cruden (1949) and Emik and Terrill (1949). If the coefficient of kinship for any pair of fully inbred individuals A,B (ϕAB) is known, then genealogical distance between A and B is G(AB)=1-ϕAB. The parental lines used in this study were chosen to represent diverse germplasm sources; hence, coefficients of kinship among them tended to be small. The transformation,

$$G^*(AB) = e^{(1-\phi AB)} - 1,$$

was used to increase separation of the matings. Jacquard (1974) suggested G*(AB) could serve as a genetic distance measure.

Statistical Procedures

Experiment I

A combined analysis across locations was carried out for each mating in which the sums of squares for generations were subdivided into single degree of freedom contrasts. The first (C1) was F_1 versus P_2, and the second (C2) was F_1 versus the midparent value which measures heterosis. The sums of squares for generation x location were subdivided into C1 x location and C2 x location.

Experiment II

The mean ($\bar{X}$) and variance (σ^2) for GYLD were calculated for each entry, and the standard error for each mean was obtained as $\sigma^2_{\bar{X}} = \sigma^2/n$, where n is the number of plants measured to obtain the mean. The heterotic deviation for an F_1 was the difference between the observed F_1 mean and the average of its parents. The standard deviation of the heterotic deviation was obtained as

$$\sigma_{heterosis} = [\sigma^2_{F_1} + 1/4(\sigma^2_{P_1} + \sigma^2_{P_2})]^{1/2}$$

where $\sigma^2_{F_1}$, $\sigma^2_{P_1}$, and $\sigma^2_{P_2}$ are the variances of the means for the F_1 and parental entries, respectively.

Experiment III

A combined multivariate analysis of variance (MANOVA) across locations, excluding the two parental entries, was carried out for the traits BWT, GYLD, and HI from each mating.

The genetic variance-covariance matrix was obtained as

$$G_{3x3} = (r\ell)^{-1}MSG_{3x3} - MSGL_{3x3},$$

where MSG_{3x3} and $MSGL_{3x3}$ are matrices of mean squares and cross products for genotypes and genotype x location interaction, respectively, and r and ℓ are the number of replicates and locations, respectively. For each mating, the matrix of eigenvalues, D_{3x3}, was obtained by solving the equation

$$D_{3x3} = O'_{3x3}G_{3x3}O_{3x3}$$

where O_{3x3} is the orthogonal matrix of eigenvectors of G, and G_{3x3} is the genetic variance-covariance matrix. The generalized genetic variance was calculated as the product of the diagonal elements of D.

Experiment IV

Multivariate analyses of variance and estimation of the genetic variance-covariance matrix and generalized genetic variances for experiment IV were computed in the same way as for experiment III.

Combined analysis of experiments III and IV

A combined analysis of variance for each mating was carried out including the parental entries using data from experiments III and IV for all traits. The standard error of an entry mean for BWT, GYLD, SYLD, or HI was

$$SE_{En} = [MS_{GE}/re]^{1/2}$$

where MS_{GE} is the mean square for genotype x location interaction, and r and e are the numbers of replications and environments, respectively. The standard error of an entry mean for HT or HD was

$$SE_{En} = [MS_E/e]^{1/2}$$

where MS_E is the mean square error and e is the number of environments (e=4 for HT and e=3 for HD). The least significant difference between the mean of a progeny and a parental mean was

$$LSD_{(.05)} = t_{.05}[2]^{1/2}SE_{En}$$

where $t_{.05}$ is the tabulated value of t at the 5% level of significance for the appropriate degrees of freedom, and SE_{En} is defined as above. Transgressive segregates were defined as F_2-derived lines whose mean performance for a trait exceeded the parental range by at least one LSD, i.e., low and high transgressive segregates had mean performance one LSD below the low parent and above the high parent for the trait, respectively.

Regression and Correlation

The relationships between genealogical distance and breeding behavior were investigated in separate analyses of variance. The observed values for heterotic deviations, numbers of transgressive segregates, and generalized genetic variances were subjected to analyses of variance, with sums of squares being subdivided into linear and quadratic regression on genealogical distance and deviations from regression. Pearson's product moment and Spearman rank correlations were calculated also.

RESULTS AND DISCUSSION

The results from experiment I are summarized in Table 3. P_1 and P_2 differed significantly for GYLD only in matings L1xL5 and L6xL8. Heterosis was significant in five matings, including Bates x Lang and all matings involving Porter. Heterosis averaged 842.3 kg/ha or 36.9% over all seven matings. There was no significant generation x location interaction.

In experiment II, heterosis averaged 3.65 gm/plant or 10.6% across the 27 matings (Table 4). Heterotic deviations exceeded twice their standard error in 10 of 27 matings with heterosis averaging 17.2% for these matings. Six matings common to experiments I and II had mean heterosis of 36.6% in the first experiment and 16.0% in the second. Heterosis was less at lower crop densities, so probably it was not due to tillering ability or other traits that have greater expression in spaced plantings. The correlation between heterotic deviations in the two experiments was positive but nonsignificant (r=0.32).

These expressions of heterosis for GYLD of oats in my experiments are consistent with previous reports (Murphy, 1966; Petr and Frey, 1967; Jenkins, 1968). Petr and Frey (1967) reported that percent yield heterosis for 15 oat matings evaluated as spaced plants ranged from 118% to 156%. Murphy (1966) evaluated 72 oat matings in spaced plantings and found mean heterosis for grain yield of 33.5%. Rothman and Bowman (1963) reported that heterosis in oats could be as high as 1636% for a single F_1, a result that may have occurred because both parents were extremely

Table 3. Parental and F_1 mean GYLD (kg/ha), standard error of the mean, heterotic deviations, and percent heterosis for oat matings grown at three locations in 1983

Mating	Generation			Heterotic deviation	% Heterosis
	P_1	P_2	F_1		
L1xL7	2011.2[a]	2179.2	3156.1±192.8	1060.9**	50.6
L1xL6	2546.4	1793.2	3191.9±230.5	1022.1**	47.1
L1xL5	2671.9	1667.7	3138.1±256.8	968.3**	44.6
L1xL4	2438.8	2582.2	2478.8±208.6	968.3**	38.6
L2xL4	3084.3	2349.1	3299.5±221.2	582.8	21.5
L3xL6	2051.4	2593.0	2779.5±229.5	457.3	19.5
L6xL8	1703.6	2869.2	3122.5±199.5	836.1*	36.6
Average	2358.2	2290.5	3166.7	842.3	36.9

[a]Standard errors for parental and F_1 means are identical.

*,**Indicate significant differences between F_1 and midparent values at the .05 and .01 levels, respectively.

Table 4. Heterotic deviation for grain yield (gm/plant) (above diagonal) and percent heterosis (below diagonal) for 27 oat matings evaluated in spaced plantings in 1984

Parent	L1	L2	L3	L4	L5	L6	L7	L8
L1	—	-3.3	0.5	3.4	5.8*	5.8*	7.1*	-1.5
L2	-8.4	—	7.9	2.2	0.1	-7.8	2.1	0.8
L3	1.2	26.9	—	5.5*	5.9*	—	6.3	-0.2
L4	8.1	6.3	17.5	—	5.5*	8.1*	4.3	9.4
L5	14.3	0.3	19.1	15.3	—	5.8*	0.5	-1.2
L6	14.3	-23.4	—	22.6	16.7	—	6.0*	12.1*
L7	17.4	6.2	20.7	12.1	1.3	17.2	—	8.1
L8	-3.7	2.4	-0.5	26.6	-3.5	35.3	23.6	—

*Indicates that heterotic deviation was at least twice as large as its standard error.

unadapted (Moll et al., 1962; Paterniani and Lonnquist, 1963; Gerrish, 1983).

The summary of the frequencies and ranges of transgressive segregates for each trait is given in Table 5. BWT, GYLD, SYLD, and HI were similar in that for each, low transgressive segregates occurred at much higher frequencies than did high transgressive segregates. This occurred because the midparent in most matings was higher than the progeny mean with the deviation being more pronounced in 1983 (experiment III) than in 1984 (experiment IV). Such a deviation could result from epistasis, from nonrandom sampling of the progeny, or from genotype by environment interaction. Dominance, if a factor, should have caused a deviation in the opposite direction since there was positive heterosis for GYLD in experiments I and II. For HD and HT, midparent values and progeny means were similar, hence high and low transgressive segregates occurred with nearly equal frequencies. The highest numbers of transgressive segregates occurred for BWT with a mean of 5.5 per mating, and the lowest numbers were observed for HI with an average of 3.7 per mating.

These results agree with those reported by Cox and Frey (1984). In interspecific oat matings, they observed much higher frequencies of low than high transgressive segregates for GYLD, whereas the converse was true for BWT, and in intraspecific matings of oats, they observed nearly equal frequencies of high and low transgressive segregates for both GYLD and BWT. Vega and Frey (1980) observed much higher frequencies of high than low transgressive segregates for GYLD in inter- and intraspecific matings

Table 5. Mean numbers of high, low, and total transgressive segregates and range for six traits observed for 28 oat matings evaluated in five environments

Trait	Mean high transgressive segregates	Range	Mean low transgressive segregates	Range	Mean total transgressive segregates	Range
BWT	0.57	0-4	4.96	0-19	5.53	0-19
GYLD	0.43	0-3	4.14	0-15	4.57	0-15
SYLD	0.61	0-7	4.32	0-21	4.93	0-21
HI	0.93	0-10	2.79	0-11	3.72	0-13
HD[a]	2.71	0-9	2.39	0-14	5.10	0-17
HT[b]	2.04	0-22	1.96	0-22	4.00	0-23
Average	1.22		3.43		4.65	

[a]HD was evaluated in three environments.

[b]HT was evaluated in four environments.

of barley (Hordeum vulgare L.), whereas they observed greater frequencies of low than high transgressive segregates for HD and HI.

Three options were available for using as many traits and as many replicates as possible to obtain a genetic variance-covariance matrix: (a) experiment III data from all replicates for BWT, GYLD, SYLD, and HI; (b) reduce the data set to one replicate at each location and include HT; or (c) reduce the data set to one replicate at locations one and two and include HT and HD. With either (b) or (c), negative variance component estimates were regularly obtained, indicating that the data lacked adequate precision. By using the entire data set for BWT, GYLD, SYLD, and HI, the genetic variance-covariance matrices were always singular. The

trait SYLD was then dropped from the analysis. Genetic variance-covariance matrices for the traits BWT, GYLD, and HI were nonsingular for most matings, however, for a few matings the smallest eigenvalue was zero or negative. The generalized genetic variance of the genetic variance-covariance matrix, which is the product of the eigenvalues, was estimated as the product of the first two eigenvalues. The natural logs for the generalized variances for the 28 matings in experiments III and IV are given in Table 6.

In experiment III, all matings had significant genetic variability as tested by Wilk's criterion in the MANOVA. By inference, the log generelized genetic variance for all matings was assumed to be significant also. The log generalized genetic variances ranged from 20.5 to 24.9 and averaged 23.0. In experiment IV, four matings (L1xL5, L1xL6, L5xL7, and L5xL8) did not show significant genetic variability as tested in the MANOVA. Their log generalized genetic variances were 12.3, 12.5, 11.0, and 9.6, respectively. The mean for all 28 matings was 21.7; however, if the four matings that lacked significant variability were excluded, the mean was 23.5. In experiment III, these four matings had values in the midrange for all matings. Perhaps the difference in estimates for them in the two experiments occurred because the genetic variance-covariance matrices were estimated with fewer observations per mean and, hence, less precision in 1984 than in 1983.

Genealogical distances between the eight parental lines are given in Table 7. Genealogical distance has a parameter range of 0.0 to 1.72, thus all matings have values in the upper one-third of the parameter range,

Table 6. Natural logs of the generalized genetic variances for 28 oat matings grown in experiment III (above diagonal) and experiment IV (below diagonal)

Parent	L1	L2	L3	L4	L5	L6	L7	L8
L1	—	23.7	21.9	24.9	22.2	23.9	23.1	24.3
L2	22.3	—	21.0	23.7	22.7	23.1	22.9	24.6
L3	22.5	23.2	—	23.3	20.5	23.9	20.8	21.1
L4	24.5	24.1	23.0	—	21.5	23.8	23.3	22.9
L5	12.3	22.4	23.7	22.8	—	22.8	22.5	22.2
L6	12.5	23.0	24.7	23.8	21.5	—	24.9	24.2
L7	23.9	23.4	24.0	24.7	11.0	24.6	—	24.4
L8	23.9	22.5	22.1	24.1	9.6	24.3	24.0	—

Table 7. Genealogical distance between the eight parental lines

Parent	L1	L2	L3	L4	L5	L6	L7	L8
L1	0	1.27	1.33	1.23	1.21	1.56	1.12	1.44
L2		0	0.48	1.27	0.50	1.56	1.12	1.21
L3			0	1.27	1.16	1.53	1.13	1.19
L4				0	1.27	1.47	1.17	1.10
L5					0	1.58	1.10	1.22
L6						0	1.47	1.40
L7							0	1.11
L8								0
	$\bar{X}$=1.23							

except L2xL3 and L2xL5, one of which is a backcross, i.e., L3 is a parent of L2. Genealogical distances between parents from the same germplasm source were lower than the mean. For example, the mean genealogical distance over all matings was 1.23, whereas the average distance between the four parents from the Iowa program was 0.92 and the distance between the two parents from the Illinois program was 1.10.

The correlations of genealogical distance with the three types of breeding behavior are presented in Table 8. Both simple and rank correlations of heterotic deviations and percent of heterosis estimated in experiments I and II with genealogical distance were negative and nonsignificant. Theoretically, with dominance for increased grain yield, the correlation of GYLD heterosis with genealogical distance should be positive. In experiment I, genealogical distances for the seven matings ranged from 1.1 to 1.6; hence, one cannot draw conclusions concerning the relationship over the entire range of this parameter. The negative association between heterotic deviation or percent of heterosis estimated in experiment II with genealogical distance may be due primarily to the large heterotic deviation of mating L2xL3. Three of the 10 matings with significant heterosis in experiment II had genealogical distances below the mean, and the genealogical distances for all 10 matings averaged 1.35. Thus, in experiment II, significant heterosis was associated with higher values of genealogical distance. In a similar study with oats, Cowen (1985) found correlations between two other measures of genetic distance and GYLD heterosis to be low to moderate and negative. Also, matings between more closely related parents tended to have significant GYLD

Table 8. Pearson product moment and Spear rank correlation of heterosis, transgressive segregates, and log generalised genetic variances with genealogical distance in an eight parent diallel of oats

Parameter	Number of observations	Pearson Product moment correlation	Spearman rank correlation
Numbers of transgressive segregates for			
BWT	28	-0.07 ns[a]	-0.01 ns
GYLD	28	-0.18 ns	-0.19 ns
SYLD	28	0.25 ns	0.22 ns
HI	28	0.26 ns	0.15 ns
HD	28	-0.18 ns	-0.21 ns
HT	28	0.44*	0.35 ns
Average	28	0.18 ns	0.14 ns
Heterosis			
deviation in experiment I	7	-0.37 ns	-0.39 ns
percent in experiment I	7	-0.29 ns	-0.43 ns
deviation in experiment II	27	-0.08 ns	-0.14 ns
percent in experiment II	27	-0.13 ns	-0.18 ns
Generalized genetic variance			
in experiment III	28	0.41*	0.42*
in experiment IV	28	-0.03 ns	0.01 ns

[a]ns indicates the correlation is nonsignificant.

*Correlation significant at the .05 level.

heterosis. A third measure of genetic distance between parents was positively correlated with GYLD heterosis, but the correlation was not significant.

The correlations for numbers of transgressive segregates for BWT, GYLD, and HD with genealogical distances were negative and nonsignificant.

Those for genealogical distance with numbers of transgressive segregates for SYLD, HI, and an average over all traits were positive and nonsignificant. Numbers of transgressive segregates for HT were significantly correlated with genealogical distances; the product moment correlation was 0.44 and the rank correlation was 0.35, a value that was significant at the 0.07 level. Fewer genes would be involved in the expression of HT than in the expression of BWT, GYLD, SYLD, or HI and, thus, less genotype by environment interaction would occur for HT. The midparent value and progeny mean for HT were nearly identical, so transgressive segregates did not result from a deviation of the progeny distribution from the parental range. Cowen (1985), working with oats, examined the correlations of numbers of transgressive segregates for these six traits with three different measures of genetic distance between parents in matings. He found no significant correlation for the traits BWT, GYLD, or SYLD, but correlations involving numbers of transgressive segregates for HI, HD, HT, and an average over all six traits were significant and both negative and positive.

The correlation of log generalized genetic variance in experiment III with genealogical distance was positive and significant, with the simple and rank correlations being 0.41 and 0.42, respectively. Log generalized genetic variance in experiment IV was uncorrelated with genealogical distance. Log generalized genetic variances estimated from experiment III were more precise than those estimated from experiment IV, so they better represent the genetic diversity of the parental lines. This precision results from greater numbers of observations per mean and, hence, higher

degrees of freedom for genotype x location interaction. Thus, genealogical distance does have a significant and positive relationship with the best genetic measure of diversity. Cowen (1985) reported that only one of the three genetic distance measures that he computed was positively correlated with log generalized genetic variances, and one was negatively correlated.

Regressions of heterosis, number of transgressive segregates, and log generalized genetic variance on genealogical distance were significant only when correlations between the pairs of variables were significant. An example is given in Table 9. Both number of transgressive segregates for HT and log generalized genetic variance from experiment III had significant linear but nonsignificant quadratic regressions. However, the R^2 values for linear regression were only 0.19 and 0.17, respectively. This corroborates the findings of Cowen (1985) who showed that of 11 significant regressions for breeding behavior onto three genetic distance measures, 10 were linear with low R^2 values.

There are some biases inherent in the estimation of genealogical distance. First, it is assumed that no selection has occurred. According to MacCluer et al. (1983), alleles that contribute to reproductive success are more likely to be identical by descent than are neutral alleles. Hence, genealogical distance probably reflects true diversity of individuals or populations only for characters that are neither directly nor indirectly subject to selection. In this study, attention was concentrated on traits that are of primary economic importance and, therefore, directly subject to selection. This causes a deviation of estimated

Table 9. Mean squares and estimates of parameters for regression of number of transgressive segregates for HT and log generalized genetic variance in 1983 onto genalogical distance of parents for 28 matings of oats

Source	df	Numbers of transgressive segregates for HT		Log generalized genetic variance in experiment III	
		MS	F	MS	F
Linear	1	199.02	6.68*	7.17	5.14*
Quadratic	1	97.86	3.28 ns	0.36	0.26 ns
Residual	25	29.80		1.39	
R^2 (linear)		0.19*		0.17*	
R^2 (quadratic after linear)		0.09		0.01	
b_L		10.48±4.23		1.99±0.86	

*Significant at the .05 level.

coefficients of kinship below the actual proportion of alleles identical by descent. The second source of bias in estimating genealogical distance arises from the assumption that no relationship existed among the original parents in the pedigrees. Again, MacCluer et al. (1983) have shown that failure to consider remote generations leads to underestimation of relationships. This bias is most pronounced in the earlier generations of the pedigree, and as the number of generations in the pedigree increases, this bias is reduced. Relationships among individuals in later generations of the pedigree result from common parentage within the known pedigree so they are fully detectable. These two sources of bias are not independent. As MacCluer et al. (1983) state, the relative importance of

recent vs. remote inbreeding, as it effects identity by descent, depends on whether or not the traits of interest have a deleterious effect on fitness.

Alleles that contribute to high yield and other agronomic traits, all of which are subject to selection, are more likely to be identical by descent than would be predicted by probabilities based on pedigrees. Hence, genealogical distance overestimates the true genetic relationship among parents in a pedigree. Genealogical distance also is biased upward by the assumption that the original parents in a pedigree are unrelated. Both sources of bias tend to cause genealogical distance to be greater than the true genetic distance, but their effects are not consistent for all pairs of parents in the pedigree. These biases might have contributed to the lack of a close association between genealogical distance and the three measures of breeding behavior in this study.

In summary, genealogical distances between parents in oat matings were negatively correlated with heterosis; however, in one experiment, significant heterosis was observed more frequently in matings of distantly related parents. Genealogical distances were positively associated with numbers of transgressive segregates for SYLD, HI, HT, and average numbers of transgressive segregates across traits. They were positively correlated with log generalized genetic variances which is a direct measure of the genetic diversity among the parents. Genealogical distances are useful to measure diversity among parents because they are easy to calculate, they can be estimated independently for pairs of parents, and they have a positive association with genetic variability.

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PART II. THE RELATIONSHIPS BETWEEN THREE MEASURES OF GENETIC DISTANCE AND HETEROSIS, TRANSGRESSIVE SEGREGATION AND GENERALIZED GENETIC VARIANCES IN OATS

ABSTRACT

Nine oat cultivars and experimental lines from four diverse germplasm sources were crossed in a diallel mating design, without reciprocals. Heterosis for grain yield was evaluated in two experiments, and 48 F_2-derived lines from each of the 36 matings were evaluated for bundle weight, grain yield, straw yield, harvest index, and heading date in two experiments. Number of transgressive segregates per trait and generalized genetic variances were calculated for each mating. Euclidean distance between parents was calculated using the first five principal components of the parental correlation matrix. The distance measures of Hanson and Casas and Cervantes et al. were calculated for each of two experiments. The relationships between the three distance measures and the three types of breeding behavior were examined via correlation and regression. Euclidean distance was negatively correlated with transgressive segregation and generalized genetic variances. Hanson and Casas' distance measure was positively correlated with transgressive segregation and generalized genetic variances. Cervantes' distance measure was negatively correlated with heterosis in one experiment. Regressions on the three distances measures, when significant, were linear. The single exception was the regression of heterosis on Euclidean distance, which had significant linear and quadratic coefficients and high R^2. No distance measure was closely associated with all three types of breeding behavior. Using information from more than one measure improved the R^2 value for polynomial regressions.

INTRODUCTION

The genetic diversity among a group of populations or genotypes may be quantified using either data on the populations per se or information obtained from diallel mating designs involving them. Measurements obtained from the populations may be used to construct a number of different genetic distance measures. Basic distance measures can be used when no correlation exists among traits. For example, Pearson's Coefficient of Racial Likeness (Pearson, 1926; Goodman, 1972) can be used for traits that are normally distributed, while Sokal's distance (Sokal, 1961; Goodman, 1972) can be used when the characters are scored on a discontinuous scale. When traits are correlated, Mahalanobis' distance (Mahalanobis, 1936; Goodman, 1967) is an appropriate measure. The axes of trait measurements may be rotated to yield a new set of orthogonal axes, while the populations maintain the same relative relationships using principal components analysis (Goodman, 1968). Euclidean distance can then be calculated using some or all of the principal component axes (Goodman, 1968; Adams, 1977).

Two procedures have been used to analyze data from diallel matings to determine relationships among the parents. The first, described by Hanson and Casas (1968), uses the parental and mating means and a group of orthogonal contrasts to locate the populations on a set of orthogonal axes after which Euclidean distance is computed. The second, described by Cervantes et al. (1978), uses correlations among the parents of a diallel based on standardized genetic effects and the distance between two parents is one minus their correlation.

Three types of breeding behavior have been shown to be related to the genetic divergence of the parental populations. Heterosis has been shown to be positively associated with genetic divergence of the parents in cotton (Gossypium spp.) (Marani, 1963; Marani and Avieli, 1973), alfalfa (Medicago spp.) (Sriwatanapongse and Wilsie, 1968), oats (Avena spp.) (Jenkins, 1968), winter wheat (Triticum aestivum L. em Thell) (Fonseca and Patterson, 1968), spring wheat (T. aestivum L. em Thell) (Sun et al., 1972), durum wheat (T. turgidum L. var. durum) (Widner and Lasbock, 1973), and maize (Zea mays L.) (Moll et al., 1962; Paterniani and Lonnquist, 1963). Greater numbers of progeny whose performance exceeded the parental range (transgressive segregates) have been observed in matings of more distantly related parents in oats (Avena spp.) (Cox, 1979; Cox and Frey, 1984) and barley (Hordeum spp.) (Vega and Frey, 1980). Goodman (1969) indicated that a direct genetic test of the degree of divergence of two compatible parents is the relative variability of their F_2. According to Goodman (1968) and Sokal (1965), the generalized variance, or determinant of the variance-covariance matrix, is the most sensitive measure of overall variability in any segregating generation.

Rodgers et al. (1983), who examined the relationship between coefficient of kinship (Malecot, 1969) and grain yield in spring oats (Avena sativa L.), found that recently developed, high-yielding cultivars displayed a broad range of variability for agronomic traits and represented several distinct sources of germplasm. These cultivars originated from four breeding programs in the midwestern USA.

In this study, I investigated the relationships between three measures of genetic distance among genotypes from the four midwestern USA oat breeding programs and heterosis, transgressive segregation, and generalized genetic variances of matings. The three distance measures used were Euclidean distance based on principal components and those proposed by Hanson and Cress (1968) and Cervantes et al. (1978). The primary objective was to determine if any of these three distances provided an adequate and appropriate measure of the diversity among genotypes from these four breeding programs.

MATERIALS AND METHODS

Nine cultivars and experimental lines of oats that originated from breeding programs in Iowa, Illinois, Indiana, and Missouri were used to initiate this study (Table 1). All nine lines produced grain yields equal to 130% of the cultivar Gopher according to Rodgers et al. (1983) and Rodgers (D. M. Rodgers, Dept. of Agronomy, Kansas State Univ., personal communication, 1981).

The nine parents were crossed in a diallel without reciprocals to produce 36 matings. In 1982, 120 F_2 seeds from each mating were space planted in the field. When mature, individual F_2 plants were harvested and threshed, and the seed from a plant was used to establish an F_2-derived line. A random set of 48 F_2-derived lines was obtained from each mating for evaluation.

In addition, sufficient F_1 seed was produced of L1xL9, L2xL5, L2xL6, L2xL7, L2xL8, L3xL5, L4xL7, and L7xL9 to conduct replicated evaluation trials. These represent matings among parents from different breeding programs.

Field Evaluation

Four separate experiments were conducted to evaluate the breeding behavior of the 36 matings, these are referred to as experiments I, II, III, and IV.

Experiment I

In 1983, three generations, the P_1, P_2, and F_1 of each of eight interprogram matings, were evaluated in a randomized complete block design

Table 1. Name or accession number, breeding program of origin, and designation of oat lines used as parents

Parent	Origin	Designation
B605-1085	Iowa	L1
Porter	Indiana	L2
D226-30-8	Iowa	L3
PI No. 469112	Iowa	L4
Ogle	Illinois	L5
CI No. 9273	Iowa	L6
Bates	Missouri	L7
CI No. 9277	Iowa	L8
Lang	Illinois	L9

with two replicates at each of three locations: (1) the Agronomy and Agricultural Engineering Field Research Center near Ames, Iowa (Agronomy Farm), (2) the Hinds Research Farm, near Ames, Iowa (Hinds Farm), and (3) the Northern Research Center near Kanawha, Iowa (Kanawha). A plot consisted of a hill sown with 20 seeds, and plots were spaced 30.5 cm apart in perpendicular directions. Each replication was bordered with two rows of hill plots to provide competition for peripheral plots. Fertilizer was applied preplant at per ha rates of 51.5 kg N and 7 kg each of P and K at Kanawha; 33.6 kg N and 51.5 kg each of P and K at the Agronomy Farm; and 84 kg N, 67.2 kg P, and 100.8 kg K at the Hinds Farm. All plots were hand weeded. To prevent foliar diseases, an eradicant fungicide, Bayleton (1-(4-chlorophenoxy)-3,3-dimethyl-1-(1H-1,2,4-

Table 2. Traits measured on a plot basis in experiments I, II, III, and IV

Trait	Designation	Definition
Heading date	HD	Number of days between June 30 and when 50% of the panicles were completely emerged
Bundle weight	BWT	Dry weight (kg/ha) of total above ground biomass
Grain yield	GYLD	Dry weight (kg/ha) of threshed grain
Straw yield	SYLD	Dry weight (kg/ha) of vegetative tissue
Harvest index	HI	Grain yield expressed as a percentage (%) of bundle weight
Height	HT	Height (cm) from ground surface to the tip of the average panicle

triazol-1-yl)-2-butone), was applied approximately one month prior to harvest.

Only grain yield (GYLD) was evaluated in experiment I (Table 2).

Experiment II

In 1984, the nine parental lines and F_1s of 35 of 36 possible matings of the diallel were evaluated in a completely randomized experiment of spaced plants at the Agronomy Farm. The F_1 of the mating L4xL7 was not included. The 44 entries were randomly assigned to plots, each parental line was planted in four plots, and an F_1 in one to three plots. A plot consisted of a row 6 m long in which plants were spaced 30 cm apart, and plots were spaced 1 m apart. Numbers of plants measured for the parents ranged from 54 to 73 with an average of 62, and numbers of plants measured

for F_1s ranged from 3 to 51 with an average of 26. Fertilizer rates per ha were 33.6 kg N and 51.5 kg each of P and K, respectively. Only grain yield (GYLD) was measured in experiment II (Table 2). Because spaced plant values were difficult to convert to kg/ha, the data were expressed as gm/plant.

Experiment III

In 1983, 48 F_2-derived lines in F_3 from each of the 36 matings and the parents each entered eight times were evaluated in a split plot design with two replicates at each of three locations: (1) the Agronomy Farm, (2) the Hinds Farm, and (3) Kanawha. Matings were assigned to main plots and F_2-derived and parental lines were assigned to subplots. The 48 F_2-derived lines and two parents of a mating were randomly assigned to the 50 subplots in a main plot. A plot consisted of a hill sown with 30 seeds, and plots were spaced 30.5 cm in perpendicular directions. A replication consisted of 1800 plots. Each replication was bordered by two rows of hill plots to provide competition for peripheral plots. Fertilizer rates and disease control measures were the same as for experiment I.

The traits bundle weight (BWT), grain yield (GYLD), straw yield (SYLD), and harvest index (HI) were measured on a plot basis on all replications at all locations; height (HT) was measured on one replication at all locations; and heading date (HD) was measured on one replication at the Agronomy and Hinds Farms (Table 2).

Experiment IV

In 1984, experiment III was repeated using F_2-derived lines in F4 with two replications, at each of two locations: (1) the Agronomy Farm and (2) Kanawha. Fertilizer rates per ha and disease control measures were identical to experiments I and III. The traits bundle weight (BWT), grain yield (GYLD), straw yield (SYLD), and harvest index (HI) were measured on a plot basis on all replications at both locations, while height (HT) and heading date (HD) were measured on one and both replications, respectively, at the Agronomy Farm (Table 2).

Statistical Procedures

Experiment I

A combined analysis across locations was carried out for each mating in which the sums of squares for generations was subdivided into single degree of freedom contrasts. The first (C1) was P_1 vs P_2, and the second (C2) was F_1 vs the midparent value, which measures heterosis. The sums of squares for generation x location was subdivided into C1 x location and C2 x location.

Experiment II

The mean ($\bar{X}$) and variance (σ^2) for GYLD were calculated for each entry and the standard error for each mean was obtained as $\sigma^2_{\bar{X}}=\sigma^2/n$ where n is the number of plants measured to obtain the mean. The heterotic deviation for an F_1 was the difference between the observed F_1 mean and the average of its parents. The standard error of the heterotic deviation was obtained as

$$\sigma_{heterosis} = [\sigma^2_{\bar{F}_1} + 1/4(\sigma^2_{\bar{P}_1} + \sigma^2_{\bar{P}_2})]^{1/2}$$

where $\sigma^2_{\bar{F}_1}$, $\sigma^2_{\bar{P}_1}$, and $\sigma^2_{\bar{P}_2}$ are the variances of the means for the F_1 and parental entries, respectively.

Experiment III

A combined multivariate analysis of variance (MANOVA) across locations, excluding the two parental entries, was carried out for the traits BWT, GYLD, and HI from each mating.

The genetic variance-covariance matrix was obtained as

$$G_{3x3} = (r\ell)^{-1}(MSG_{3x3} - MSGL_{3x3})$$

where MSG_{3x3} and $MSGL_{3x3}$ are matrices of mean squares and cross products for genotypes and genotype x location interaction, respectively, and r and ℓ are the numbers of replicates and locations, respectively. For each mating, the matrix of eigenvalues, D_{3x3}, was obtained by solving the equation

$$D_{3x3} = O'_{3x3}G_{3x3}O_{3x3}$$

where O_{3x3} is the orthogonal matrix of eigenvectors of G, and G_{3x3} is the genetic variance-coverience matix. The generelized genetic variance was calculated as the product of the diagonal elements of D.

Experiment IV

Multivariate analyses of variance and estimation of the genetic variance-covariance matrix and generalized genetic variances for experiment IV were computed in the same way as for experiment III.

Combined analysis of experiments III and IV

A combined analysis of variance for each mating was carried out including the parental entries using data from experiments III and IV for all traits. The standard error of an entry mean for BWT, GYLD, SYLD, or HI was

$$SE_{En} = [MS_{GE}/re]^{1/2}$$

where MS_{GE} is the mean square for genotype by environment interaction, and r and e are the numbers of replications and environments, respectively. The standard error of an entry mean for HT or HD was

$$SE_{En} = [MS_{E}/e]^{1/2}$$

where MS_{E} is the mean square error and e is the number of environments (e=4 for HT and e=3 for HD). The least significant difference between the mean of a progeny and a parental mean was

$$LSD_{(.05)} = t_{.05}[2]^{1/2}SE_{En}$$

where $t_{.05}$ is the tabulated value of t at the 5% level of significance for the appropriate degrees of freedom, and SE_{En} is defined as above. In my study, a transgressive segregate was defined as an F_2-derived line whose mean performance for a trait exceeded the parental range by at least one LSD, i.e., low and high transgressive segregates for a trait had mean performance one LSD below the low parent and above the high parent, respectively.

Calculation of Distance Measures

A data set for the nine parents was constructed using the six traits measured in this study plus protein percentage, groat percentage, test weight, lodging score, barley yellow dwarf virus reaction, and mean rust reaction. Protein percentage, groat percentage, and barley yellow dwarf virus reaction were transformed to the arc sine, arc sine, and square root, respectively, prior to analysis. A principal component analysis was carried out on the correlation matrix of the 12 traits. The first five principal components of the correlation matrix accounted for over 94% of the total variation. All had eigenvalues greater than 0.87, with a mean of 2.27. Euclidean distance (designated DI) between parents was calculated using the first five principal component axes. Euclidean distance was calculated as the square root of the sum of the squared differences between the parents on each axis.

The distance measures of Hanson and Casas (1968) and Cervantes et al. (1978) were calculated using data from experiments III and IV. Hanson and Casas' (1968) distance measure (designated DII) was calculated after obtaining a nine by nine matrix of parental and mating means for GYLD from each experiment. These were multiplied by a nine by eight matrix whose columns were the orthogonal polynomials of degree one to eight for nine equally spaced treatments. This located the nine parents on a set of eight orthogonal axes. The location of each parent was standardized on each axis after which Euclidean distance was computed.

To obtain the distance measure of Cervantes et al. (1978) (designated DIII), general combining ability (GCA) effects for each parent were

calculated as the mean deviation of all matings involving a given parent from the grand mean for the trait. The GCA effects were standardized for each trait and used to calculate the correlations between parents. The genetic distance between two parents was defined as one minus their correlation.

Regression and Correlation

The relationships between the distance measures and breeding behavior were investigated in separate analyses of variance. The observed values for heterotic deviations, numbers of transgressive segregates, and generalized genetic variances were subjected to analyses of variance, with the sums of squares being subdivided into linear and quadratic regression upon a distance measure and deviations from regression. Polynomial regression analysis was conducted, and the sums of squares were subdivided into portions due to regression and deviations from regression. Pearson's product moment and Spearman rank correlations were computed among all combinations of distance measures and breeding behavior measures.

RESULTS AND DISCUSSION

In experiment I, P_1 and P_2 differed significantly for GYLD only in matings L2xL6 and L7xL9 (Table 3). Heterosis was significant in five matings including Bates x Lang and all of those involving Porter. Heterosis averaged 793 kg/ha or 34.5% over the eight matings. There was no significant generation x location interaction.

In experiment II, heterosis avereged 4.43 gm/plant, or 12.9% across the 35 matings (Table 4). Heterotic deviations exceeded twice their standard error in 16 of 35 matings with heterosis avereging 21.4% for these matings. Seven matings common to experiments I and II had mean heterosis of 36.6% in the first experiment and 15.2% in the second. Heterosis was least at low crop densities, and hence it probably was not due to tillering or any trait that had greater expression in spaced plantings. The correlation between heterotic deviations observed in the two experiments was positive but low and nonsignificant (r=0.40).

The expression of heterosis for GYLD in oats in my experiments are consistent with previous reports (Murphy, 1966; Petr and Frey, 1967; Jenkins, 1968). Petr and Frey (1967) found that percent heterosis for GYLD for 15 oat matings evaluated as spaced plants ranged from 118% to 156%. Murphy (1966) evaluated 72 oat matings in spaced plantings and found mean heterosis for GYLD of 33.5%. Rothman and Bowman (1963) reported that heterosis in oats could be as high as 1636% for a single F_1, a result that may have occurred because both parents were extremely unadapted (Moll et al., 1962; Paterniani and Lonnquist, 1963; Gerrish, 1983).

Table 3. Mating, parental and F_1 mean GYLD (kg/ha), standard errors of mean, heterotic deviation, and percent heterosis for eight oat matings grown at three locations in 1983

Mating	P_1	P_2	F_1	Heterotic deviation	% heterosis
L1xL9	2438.8+	2689.9	3012.6±246.7	448.25	17.5
L2xL8	2011.2	2179.2	3156.1±192.8	1060.9**	50.6
L2xL7	2546.4	1793.2	3191.9±230.5	1022.1**	47.1
L2xL6	2671.9	1667.7	3138.1±256.8	968.3**	44.6
L2xL5	2438.8	2582.2	3478.8±208.6	968.3**	38.6
L3xL5	3084.3	2349.1	3299.5±221.2	582.8	21.5
L4xL7	2051.4	2593.0	2779.5±229.5	457.3	19.5
L7xL9	1703.6	2869.2	3122.5±199.5	836.1*	36.6
Average	2368.3	2340.4	3147.4	793.0	34.5

+Standard errors for parental and F_1 means are identical.

*,**Indicate significant differences between F_1 and midparent values at the 0.05 and 0.01 levels, respectively.

The frequencies and range of transgressive segregates for BWT, GYLD, SYLD, and HI were similar in that for each, low transgressive segregates occurred at much higher frequencies than did high transgressive segregates (Table 5). This occurred because the midparent value for these traits in most matings was higher than the progeny mean. The deviation was more pronounced in 1983 (experiment III) than in 1984 (experiment IV). Such a deviation could result from epistasis, from nonrandom sampling of the progeny, or from genotype by environment interaction. Dominance, if a factor, should cause a deviation in the opposite direction for GYLD since there was positive heterosis for GYLD in experiments I and II. For HD and

Table 4. Heterotic deviation for grain yield (gm/plant) (above diagonal) and percent heterosis (below diagonal) for 35 oat matings evaluated in space plantings in 1984

Parent	P1	P2	P3	P4	P5	P6	P7	P8	P9
P1	—	0.15	4.5*	6.0*	12.7*	8.6*	14.8*	6.2*	3.8
P2	0.4	—	-3.3	0.5	3.4	5.8*	5.8*	7.1*	-1.5
P3	13.3	-8.4	—	7.9	2.2	0.1	-7.8	2.1	0.8
P4	19.4	1.2	26.9	—	5.5*	5.9*	—	6.3	-0.2
P5	35.4	8.1	6.3	17.5	—	5.5*	8.1*	4.3	9.4
P6	24.4	14.3	0.3	19.1	15.3	—	5.8*	0.5	-1.2
P7	42.1	14.3	-23.4	—	22.6	16.7	—	6.0*	12.1*
P8	17.8	17.4	6.2	20.7	12.1	1.3	17.2	—	8.1
P9	10.9	-3.7	2.4	-0.5	26.6	-3.5	35.3	23.6	—

*Indicates that the heterotic deviation was at least twice as large as its standard error.

Table 5. Mean numbers of high, low, and total transgressive segregates and range for six traits observed for 36 oat matings evaluated in five environments

Trait	Mean high transgressive segregates	Range	Mean low transgressive segregates	Range	Mean total transgressive segregates	Range
BWT	0.44	0-4	4.64	0-19	5.08	0-19
GYLD	0.28	0-3	4.03	0-15	4.31	0-15
SYLD	0.53	0-7	4.19	0-21	4.72	0-21
HI	1.00	0-10	2.97	0-16	3.97	0-16
HD[a]	3.75	0-13	2.28	0-14	6.03	0-17
HT[b]	2.22	0-22	1.78	0-22	4.00	0-23
Average	1.37		3.32		4.69	

[a]HD was evaluated in three environments.

[b]HT was evaluated in four environments.

HT, midparent values and progeny means were similar and, as expected, high and low transgressive segregates occurred with nearly equal frequencies. The highest numbers of total transgressive segregates occurred for HD with a mean of 6.0 per mating and the lowest numbers were observed for HI with an average of 4.0 per mating.

These results agree with those reported by Cox and Frey (1984). In interspecific oat matings, they observed much higher frequencies of low than high transgressive segregates for GYLD, while the converse was true for BWT. In intraspecific matings, there were nearly equal frequencies of high and low transgressive segregates for both GYLD and BWT. Vega and Frey (1980) observed much higher frequencies of high than low

transgressive segregates for GYLD in inter- and intraspecific matings of barley (Hordeum vulgare L.), whereas they observed greater frequencies of low than high transgressive segregates for HD and HI.

Three options were available for using as many traits and as many replicates as possible to obtain a genetic variance-covariance matrix: (a) using all experiment III data from all replicates for BWT, GYLD, SYLD, and HI, (b) reduce the data set to one replicate at each location and include HT, or (c) reduce the data set to one replicate at the Agronomy and Hinds Farms and include HT and HD. With either (b) or (c), negative variance component estimates were obtained regularly indicating that the data lacked adequate precision. By using the entire data set for BWT, GYLD, SYLD, and HI, the genetic variance-covariance matrices were always singular. The trait SYLD was then dropped from the analysis. Genetic variance-covariance matrices for the traits BWT, GYLD, and HI were nonsingular for most matings; however, for a few matings the smallest eigenvalue was zero or negative. The generalized genetic variance of the genetic variance-covariance matrix, which is the product of the eigenvalues, was estimated as the product of the first two eigenvalues. The natural logs of the generalized genetic variance for each of the 36 matings in experiments III and IV are given in Table 6.

In experiment III, all matings had significant genetic variability as tested by Wilks' criterion in the MANOVA. By inference, the log generalized genetic variances for all matings were assumed to be significant also. Natural logs of the generalized genetic variance ranged from 20.5 to 24.9, averaging of 23.0. In experiment IV, eight matings (L1xL2,

Table 6. Log generalized genetic variances for 36 oat matings grown in experiment III (above diagonal) and experiment IV (below diagonal).

Parent	L1	L2	L3	L4	L5	L6	L7	L8	L9
L1	—	22.6	24.0	21.6	23.6	22.0	22.2	24.2	24.0
L2	12.9	—	23.7	21.9	24.9	22.2	23.9	23.1	24.3
L3	23.4	22.3	—	21.0	23.7	22.7	23.1	22.9	24.6
L4	6.3	22.5	23.2	—	23.3	20.5	23.9	20.8	21.1
L5	22.3	24.5	24.1	23.0	—	21.5	23.8	23.3	22.9
L6	13.6	12.3	22.4	23.7	22.8	—	22.8	22.5	22.2
L7	23.6	12.5	23.0	24.7	23.7	21.5	—	24.9	24.2
L8	12.4	23.9	23.4	24.0	24.7	11.0	24.6	—	24.4
L9	22.8	23.9	22.5	22.1	24.1	9.6	24.3	24.0	—

L1xL4, L1xL6, L1xL8, L2xL6, L2xL7, L6xL8, and L6xL9) did not show significant variability as tested in the MANOVA. Their natural log generalized genetic variances were 12.9, 6.3, 13.6, 12.4, 12.3, 12.5, 11.0, and 9.6, respectively. The mean value for all 36 matings was 20.7; however, if the eight matings that lacked significant variability were excluded, the mean was 23.4. In 1983, these eight matings had values in the midrange for all matings. The difference in estimates for these eight matings for the two years could have resulted from differences in locations, year effects, or precision of experimentation.

DI between the nine parents ranged from 1.6 to 7.4 with an average of 4.6 (Table 7). The two lines from the Illinois program, L5 and L9, were more closely related than the average, whereas the five lines from the Iowa program, L1, L3, L4, L6, and L8, were less closely related than the average, with a mean distance among them of 4.7.

Table 7. DI based on the first five principal components of the phenotypic correlation matrix for the nine oat parents

Parent	L2	L3	L4	L5	L6	L7	L8	L9
L1	4.4	2.7	4.7	3.7	4.2	5.1	5.1	3.1
L2		5.9	7.2	4.7	4.4	5.1	4.9	5.5
L3			5.8	3.5	5.3	4.9	4.6	1.6
L4				7.4	5.3	5.8	6.5	4.9
L5					3.9	4.6	4.2	3.9
L6						4.3	3.4	4.6
L7							4.3	3.6
L8								3.8

In experiment III, the DII distances between parents ranged from 1.9 to 6.5 with an average of 3.8, while in experiment IV, they ranged from 1.9 to 6.8 with an average of 3.9 (Table 8). The two lines from Illinois had distance of 4.4 and 4.1 in experiments III and IV, respectively, and average distances between lines from Iowa were 4.3 and 4.9 in experiments III and IV, respectively. All of these values were above the corresponding experiment means.

The theoretical parameter range for the distance measure proposed by Cervantes et al. (1978) is 0 to 2.0. In experiment III, DIII distances between the parents ranged from 0.1 to 1.9 with an average of 1.1, whereas for experiment IV they ranged from 0.1 to 2.0 with an average of 1.1 (Table 9). In both years, the distances covered nearly the entire possible range of values. The two lines from Illinois were more closely related than the average for all nine parents in both experiments, while

Table 8. DII distances between nine oat lines for experiment III (above diagonal) and experiment IV (below diagonal)

Parent	L1	L2	L3	L4	L5	L6	L7	L8	L9
L1		3.8	6.0	2.7	3.6	3.7	2.5	4.1	3.3
L2	2.5		5.0	3.9	3.5	2.7	3.5	2.1	3.3
L3	4.5	3.7		4.7	4.0	6.0	5.3	5.3	6.5
L4	3.6	4.6	6.8		3.8	4.3	2.1	4.1	4.5
L5	2.7	2.6	3.0	4.8		3.9	4.3	4.2	4.4
L6	2.9	2.8	4.1	4.8	2.9		3.5	2.1	1.9
L7	4.1	2.6	4.6	5.8	4.0	3.9		3.3	3.8
L8	2.8	3.0	3.6	4.8	2.6	1.9	4.5		3.0
L9	4.2	3.8	4.8	5.1	4.1	3.3	5.8	2.9	

Table 9. DII distances between nine oat lines for experiment III (above diagonal) and experiment IV (below diagonal)

Parent	L1	L2	L3	L4	L5	L6	L7	L8	L9
L1		1.1	0.8	1.3	0.2	1.6	0.9	1.4	0.9
L2	0.3		1.6	1.7	0.7	1.2	0.3	1.0	1.4
L3	1.6	1.8		0.6	0.9	1.6	1.1	1.8	0.5
L4	1.8	1.9	0.2		1.7	0.8	1.9	0.8	1.2
L5	0.1	0.5	1.3	1.7		1.7	0.4	1.6	0.7
L6	1.0	0.6	1.8	1.4	1.3		1.3	0.1	1.1
L7	0.4	0.3	2.0	1.8	0.6	0.2		1.5	0.6
L8	1.8	1.4	0.3	0.3	1.8	1.3	1.8		1.6
L9	1.0	1.2	1.0	1.2	0.6	1.2	0.9	1.4	

the average distance between lines from the Iowa program was nearly identical to the mean in each experiment.

The correlations of the three types of breeding behavior with the distance measures are shown in Table 10. DI was negatively correlated with numbers of transgressive segregates for each trait and when averaged over all traits. Correlations of DI with numbers of transgressive segregates for BWT, GYLD, and SYLD were low and nonsignificant ranging from -.14 to -.26, whereas the correlations for HI was moderate and highly significant. DI was moderately correlated with numbers of transgressive segregates for HD with the simple correlation being significant ($r=-0.34^{**}$). The product moment correlation of DI with numbers of transgressive segregates for HT was low and nonsignificant, but the rank correlation was nearly twice as large and significant. Rank correlations may detect relationships that are not linear. DI was significantly associated with average numbers of transgressive segregates via both simple and rank correlations. Transgressive segregates will occur more frequently when the parental range is much smaller than the progeny range. Since DI is based on parental performance, parents that are distantly related will be widely separated for any given trait; hence, transgressive segregates are unlikely to occur. Numbers of transgressive segregates were positively associated with log generalized genetic variances, while DI was negatively correlated with log generalized genetic variances. The relationships of DI with parental range and log generalized genetic variances both contribute to the negative correlation of DI with numbers of transgressive segregates.

Table 10. Pearson product moment and Spearman rank correlations of numbers of transgressive segregates, heterosis, and generalized genetic variances with DI, DII, and DIII distances for 36 matings of oats

Parameter	n	Experiment III (1983)						Experiment IV (1984)			
		DI		DII		DIII		DII		DIII	
		r	r_{rank}	r	r_{rank}	r	r_{rank}	r	r_{rank}	r	r_{rank}
Numbers of transgressive segregates for											
BWT	36	-.23	-.26	0.18	0.13	-.07	-.09	-.19	-.20	0.23	0.18
GYLD	36	-.14	-.13	0.17	0.26	-.07	-.05	-.16	-.12	0.22	0.24
SYLD	36	-.26	-.31	0.07	0.02	-.28	-.24	-.18	-.22	0.04	0.04
HI	36	-.46**	-.46**	0.36*	0.34*	-.17	-.15	0.03	-.02	-.13	-.21
HD	36	-.34*	-.30	0.40*	0.48**	-.24	-.24	0.20	0.16	-.07	-.10
HT	36	-.19	-.35*	0.11	0.01	-.18	-.21	0.14	-.17	0.05	0.07
Average	36	-.45**	-.39*	0.34*	0.38*	-.30	-.25	-.04	-.05	0.09	0.10
Heterosis deviation in experiment I	8	0.31	0.48	-.04	-.05	-.54	-.31	-.58	-.55	-.58	-.40
percent in experiment I	8	0.36	0.45	-.16	-.12	-.47	-.21	-.51	-.50	-.51	-.38
deviation in experiment II	35	-.11	-.13	-.30	-.23	-.28	-.29	0.05	0.03	-.44**	-.37*
percent in experiment II	35	-.08	-.09	-.27	-.18	-.27	-.28	0.11	0.10	-.44**	-.38*
Generalized genetic variance in											
experiment III	36	-.36*	-.31	0.06	-.04	-.06	-.09	-.17	-.11	0.15	0.17
experiment IV	36	0.06	0	0.37*	0.11	0.09	0.03	0.47**	0.33*	0.02	0.10

*,** Indicate correlation coefficients significant at the 0.05 and 0.01 levels, respectively.

DII distances from experiment III were positively correlated with numbers of transgressive segregates for all traits and for the average over traits. In 1983, simple and rank correlations of DII with numbers of transgressive segregates for BWT, GYLD, SYLD, and HT were low and nonsignificant. The DII correlations with numbers of transgressive segregates for HI, HD, and the average over all traits were positive, moderate, and significant. In experiment IV, DII was not significantly correlated with numbers of transgressive segregates for any trait or for the average over traits.

In experiment III, DIII was negatively correlated with numbers of transgressive segregates for all traits and the average over all traits. The correlations ranged from -0.07 to -0.28 and none was significant. In contrast, DIII from experiment IV was positively correlated with numbers of transgressive segregates for BWT, GYLD, SYLD, HT, and the average over all traits, and negatively correlated with numbers of transgressive segregates for HI and HD. However, no DIII correlation in 1984 was significant.

No correlation was significant for any distance measure with numbers of transgressive segregates for BWT, GYLD, or SYLD, probably because the progeny means deviated so much from the midparent values. The deviations were less pronounced for HT, HD and HI, and correlations of numbers of transgressive segregates for these traits and the average over all traits with two distance measures were significant. The year or set of environments in which the experiment was conducted had a great influence upon the relationship between a distance measure and the numbers of transgressive

segregates. DII and DIII were more closely associated with numbers of transgressive segregates for HI, HD, HT, and the average over all traits in 1983 than in 1984. Three of five evaluation environments used to define transgressive segregates were testing sites in 1983.

Heterosis in experiment I was more extensively and precisely determined than in experiment II; however, the low number of matings evaluated in 1983 probably precluded the occurrence of significant correlations. Only DI was positively correlated with either heterotic deviation or percent of heterosis in experiment I. Except for DII from experiment III, all distance measures were moderately correlated with both heterotic deviations and percent of heterosis, and both DII and DIII from experiment IV were more highly correlated with heterotic deviation or percent of heterosis than they were from experiment III. Rank correlations were the same in sign but smaller in magnitude than the simple correlations except for DI.

Correlations of DI with heterotic deviation and percent of heterosis in experiment II were negative and nonsignificant. DII from experiment III was more highly negatively correlated with both heterotic deviation and percent of heterosis for experiment II than for experiment I, and DII from experiment IV showed no correlation with either heterotic deviation or percent of heterosis. DIII from both experiments III and IV was negatively correlated with heterotic deviation and percent of heterosis from experiment II, and the correlations for DII from experiment IV were significant.

Generally, correlations of distance measurements with heterotic expressions were of smaller absolute magnitude for experiment II than for experiment I. Heterosis was not measured as precisely in experiment II. For the 16 matings that had significant heterosis in experiment II, mean distance values for all were below the mean of all matings. Cowen (1985) has found that significant heterosis for GYLD of oats was associated with larger values for genealogical distance between the parents. No correlation was given by Hanson and Casas (1968), but they reported a close linear relationship between heterosis and DII; however, the data used to calculate both were identical. Ghaderi et al. (1984) examined the correlation between heterosis for seed yield and Mahalanobis' D^2 distance for dry bean (Phaseolus vulgaris L.) and faba bean (Vicia faba L.). With dry bean, the correlation was positive (r=0.73), while with faba bean, the correlation was positive in one year (r=0.18) and negative in a second (r=-.29).

As with transgressive segregation, the relationship of a given distance measure with heterosis for GYLD depended to a great extent on the data set used to estimate the distance measure. As examples, DII from experiment III was negatively correlated with heterosis in experiment II, whereas when from experiment IV they were uncorrelated; and, DIII from experiment III and IV was negatively correlated with heterosis in experiment II but with quite different magnitudes.

Log generalized genetic variance is considered to be the best measure of the genetic diversity of two parents in a mating. Because the data set for experiment III was more extensive and all matings had significant

genetic variability, log generalized genetic variances calculated from this experiment probably were a good representation of the true diversity of the parents. DI was the only distance measure that was significantly correlated with log generalized genetic variances from experiment III. Both simple and rank correlations were moderate and negative. DII and DIII from experiment IV gave zero or positive correlations with log generalized genetic variances, but most were low and only three were significant. The matings without significant genetic variability in experiment IV had mean values for DII below the mean of all matings in both 1983 and 1984. DIII from either experiment III or IV was uncorrelated with log generalized genetic variances in experiment IV. Although log generalized genetic variances from experiment III probably provided the best measure of the genetic diversity between parents, log generalized genetic variances for experiment IV also should have been reasonable measures of this diversity. Interestingly, the relationships of DII and DIII with log generalized genetic variances from experiment IV were more consistent over year of estimation. DII was positively correlated for both 1983 and 1984, while DIII was uncorrelated for both 1983 and 1984.

Linear and quadratic regressions were computed for all combinations of distance measures and breeding behavior and those that showed significance for either linear or quadratic regressions are presented in Table 11. With two exceptions, significant regressions were obtained only for combinations that showed significant correlations (Table 10). Regressions of numbers of transgressive segregates for HI, HD, and average over traits onto DI were negative and linear with linear R^2 values of 0.22, 0.12 and

Table 11. Regression of breeding behavior on three distance measures. Significance of linear and quadratic after linear sources of variation, R^2 values, regression coefficients and their standard errors

Dependent var.	Independent var.	Linear R^2	Quadratic after linear R^2	b_L	b_Q
Transgressive segregates for HI	DI	0.22**	0	-1.56±0.51	—
Transgressive segregates for HD	DI	0.12*	0	-1.48±0.71	—
Transgressive segregates average	DI	0.20**	0.03	-1.11±0.38	—
Transgressive segregates for HI	DII from exp. III	0.13*	0.01	1.23±0.55	—
Transgressive segregates for HD	DII from exp. III	0.16*	0.01	1.78±0.71	—
Transgressive segregates average	DII from exp. III	0.12*	0	0.87±0.41	—
Heterotic dev. experiment II	DIII from exp. IV	0.20**	0	-3.42±1.2	—
Percent heterosis experiment II	DIII from exp. IV	0.19**	0	-9.72±3.5	—
Log generalized gen. var. experiment III	DI	0.13*	0.02	-0.37±0.17	—

Table 11. Continued

Dependent var.	Independent var.	Linear R^2	Quadritic after linear R^2	b_L	b_Q
Log generalized gen. var. experiment IV	DII from exp. III	0.14*	0.03	1.73±0.75	—
Log generalized gen. var. experiment IV	DII from exp. IV	0.22**	0.04	2.24±0.72	—
Heterotic dev. experiment I	DI	0.09	0.77**	2832±528	-314.5±60.3
Percent heterosis experiment I	DI	0.13	0.64**	134.8±34.5	-14.8±3.9

*,** Indicate regressions significant at the 0.05 and 0.01 levels, respectively.

0.20, respectively. In contrast, regressions of these three variables on DII from experiment III were significant, positive, and linear. R^2 values for linear regression were 0.13, 0.16, and 0.12, respectively. The regression of heterotic deviation from experiment II on DIII from experiment IV was negative with R^2=0.20 for linear fit. Regression of percent heterosis in experiment II was also significant. Regression of log generalized genetic variances from experiment III on DI was linear and negative. In contrast, regression of log generalized genetic variances from experiment IV on DII from both experiments were linear, positive, and significant. The regression on DII from 1984 had both a larger regression coefficient and R^2 than that for DII from 1983. This result was expected because the year and location effects were similar for log generalized genetic variances estimated from experiment IV and DII from 1984. Cowen (1985) found a significant, positive, and linear regression of log generalized genetic variances on genealogical distance.

The correlation of heterotic deviation from experiment I with DI was not significant, but the regression was. In contrast to all other significant regressions, this relationship was quadratic. The R^2 value for fitting the linear regression was nonsignificant, whereas the R^2 for linear plus quadratic was highly significant. Both the linear and quadratic regression coefficients were significant with the linear one being positive and the quadratic one being negative (Table 11). Heterotic deviations were negative or zero until the distance between the parents was at least 2.7, they would reach a maximum at a distance of 4.5 and drop to zero when the distance between the parents was approximately 6.3

(Figure 1). The regression of percent heterosis from experiment I on DI was similar to Figure 1 and will not be shown. These results are similar to those of Moll et al. (1965) with maize, even though a more limited range in diversity was examined in this study. Isleib and Wynne (1983) examined the regression of heterotic deviation for seed yield on DI for 27 matings of peanut (Arachis hypogaea L.) and obtained a positive linear regression with a nonsignificant quadratic component.

Polynomial regressions of average transgressive segregation over all traits, heterotic deviation in experiment II, and log generalized genetic variances from experiments III and IV upon linear and quadratic functions of all three distance measures were computed. These analyses were conducted to determine if variability for any of these three types of breeding behavior could be explained more completely by using more than a single distance measure. R^2 values were moderate for fit of first and second order polynomial regression on all three measures estimated in both years (Table 12). For heterotic deviations in experiment II, average transgressive segregation, and log generalized genetic variances in experiments III and IV, the R^2 values were 0.42, 0.52, 0.27, and 0.38, respectively. By including more than one distance measure or a distance measure estimated in two years in the regression, R^2 values for fit of the model were higher; however, when all measures were included in the regression, never more than approximately half of the variability was explained by the model.

Although all three types of breeding behavior evaluated in this study have been shown to be positively associated with genetic diversity of the

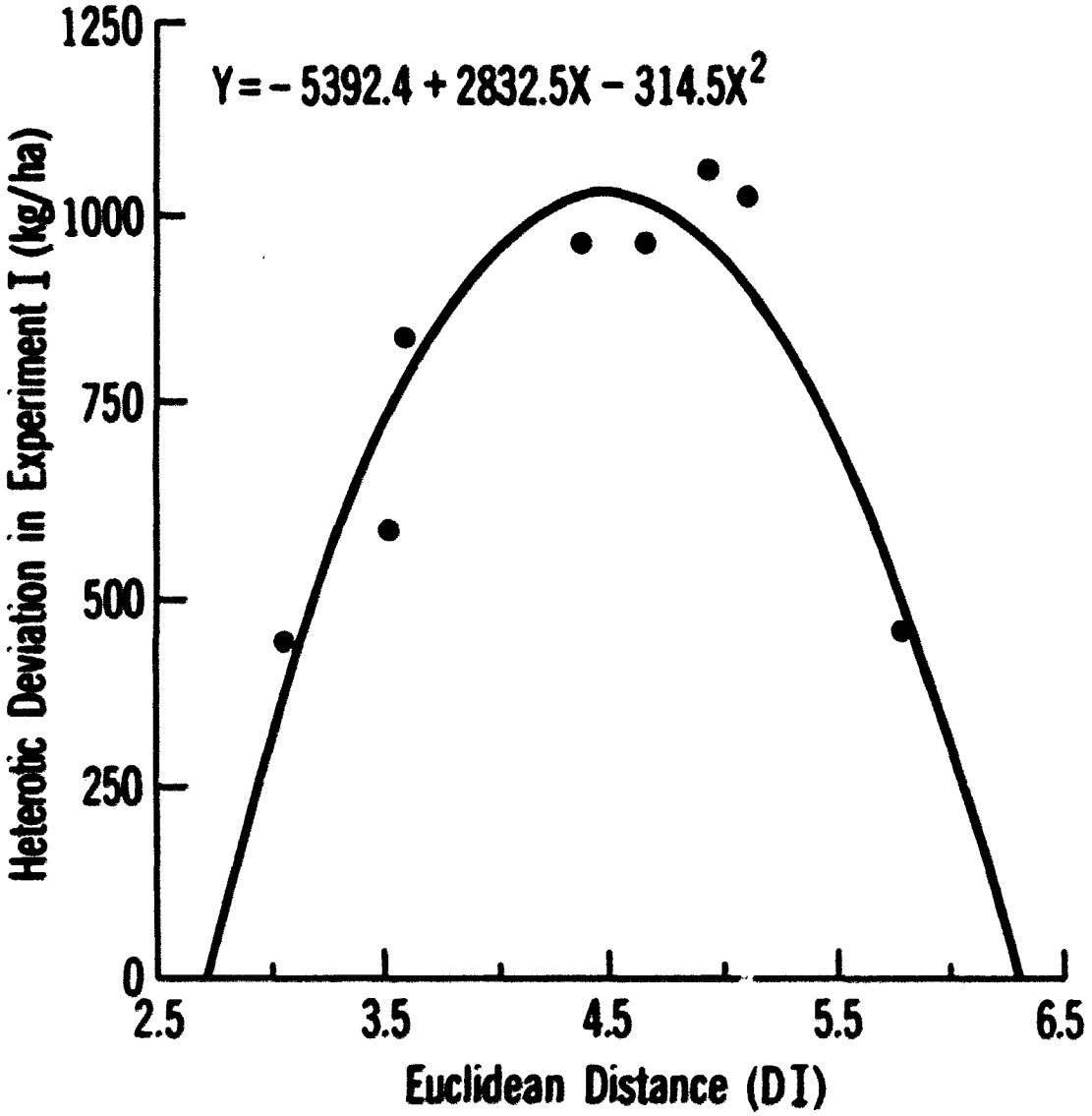

Figure 1. Regression of heterotic deviations (kg/ha) from experiment I

Table 12. Dependent variable, independent variables, and R^2 values for polynomial regression of three types of breeding behavior on three distance measures

Dependent variable	Independent variables	R^2
Transgressive segregates averaged across traits	Linear and quadratic for DI, DII, and DIII, 1983 and 1984	0.52**
Transgressive segregates averaged across traits	DI linear and quadratic, DII, 1983 linear, DIII, 1983 linear and DIII, 1984 quadratic	0.49**
Heterotic deviation from experiment II	Linear and quadratic for DI, DII, and DIII, 1983 and 1984	0.42ns
Heterotic deviation from experiment II	DI linear, DII and DIII, 1984 linear, and DIII, 1983 quadratic	0.35**
Log generalized gen. var. from experiment III	Linear and quadratic for DI, DII, and DIII, 1983 and 1984	0.27ns
Log generalized gen. var. from experiment III	DI linear and DIII, 1984 quadratic	0.18*
Log generalized gen. var. from experiment IV	Linear and quadratic for DI, DII, and DIII, 1983 and 1984	0.38ns
Log generalized gen. var. from experiment IV	DII, 1983 linear and quadratic DII, 1984 linear and quadratic	0.33**

ns,*,**Indicate that polynomial regression was nonsignificant or significant at the 0.05 and 0.01 levels, respectively.

parents in matings, they are not entirely consistent as measures of this diversity. Transgressive segregation was positively associated with log generalized genetic variances, but heterosis had little or no relationship with either of them. Therefore, it is not surprising that no measure of genetic distance was closely associated with all three types of breeding behavior. DI and DII were correlated with both numbers of transgressive

segregates and log generalized genetic variances and not with heterosis, but the opposite was true for DIII. No distance measure was positively associated with log generalized genetic variance from experiment III, which was the best direct genetic test of the diversity among parents. Contrarily, DI had a significant negative correlation with it. DII was positively correlated with log generalized genetic variance from experiment IV which also was a reasonable measure of the diversity present.

For thirteen combinations, regressions of breeding behavior upon a distance measure were signficant even though the R^2 values were small. Eleven of these regressions were linear and heterosis in experiment I upon DI was quadratic. Polynomial regressions that included more than a single distance measure gave higher R^2 values, but even when linear and quadratic functions of all distance measures were included, the R^2 values were never greater than circa 0.5.

DII and DIII were estimated separately for the two years. The relationship of both distance measures with the three types of breeding behavior depended to a considerable extent on the year of estimation. There were changes in both the sign and magnitude of the correlations of DII and DIII with the three types of breeding behavior from year to year. All data sets used in this study included more than one location and the number of observations per mean was large. To circumvent the inconsistencies found herein, data sets used to estimate the three distance measures should include several years and several locations per year. Additionally, both DI and DIII require data on a large number of traits with moderate to high heritabilities.

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SUMMARY AND CONCLUSIONS

The results of Parts I and II have implications in oat breeding that can be roughly subdivided into (a) development of breeding populations, (b) development of hybrid cultivars, and (c) monitoring the diversity among cultivated genotypes.

Prior to the production of actual breeding populations, a breeder may consider numerous possible parental combinations and will mate those parents that have the greatest probability of giving a population the desired mean performance and genetic variance. In the absence of epistasis, mean performance of inbred generations of a single cross can be reasonably well-predicted by midparent values, and of a more complex mating by the means of the parents weighted by their relative contributions to the mating. Genetic variance of a population will be closely associated with the genetic diversity of the parents. The most desirable measure of genetic diversity must be easily calculated, closely associated with population genetic variances, and such that it can be estimated for any pair of parents independently of all other parents considered. Three measures of genetic diversity used in this study had signficiant relationships with population genetic variances. Of these, both genealogical distance and Euclidean distance were more easily calculated than Hanson and Casas' distance. The negative relationship of Euclidean distance with population genetic variances discounts its possible value. Genealogical distance, although it does not have an extremely close relationship with population genetic variances, does satisfy the other two requirements and is likely the best measure of the four considered.

Should the technology for the economical production of hybrid oat seed become available, oat breeders will need some basis for the selection of parents to produce hybrids. This would allow the breeder to concentrate evaluation efforts where the potential for hybrid performance is greatest. The very close association of heterosis with Euclidean distance does provide an objective criterion for the selection of parents. Pairs of parents which have intermediate values for Euclidean distance are most likely to give the highest F_1 heterosis.

Finally, breeders have as a goal to maintain or increase the amount of diversity among cultivars of a species. Without a quantified measure of diversity, it is impossible for breeders to measure their success in attaining this goal. Although no measure of diversity examined in this study is ideally suited to this purpose, the ease of calculation of genealogical distance, as well as its independence from evaluation experiments, suggests that it is the best measure among those considered in this study.

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